Agricultural Systems, 53 (1997) pp. 1–25

PII: S0308-521X(96)00039-X 0308-521X/97 $17.00+0.00

Predicting Empty Body Composition and Composition of Empty Body Weight Changes in Mature Cattle

C. B. Williams* & T. G. Jenkins

Roman L. Hruska US Meat Animal Research Center, ARS, USDA, P.O. Box 166, Clay Center, Nebraska 68933–0166, USA

(Received 17 April 1996)

ABSTRACT

Data on empty body chemical composition of 18 breeds or breed crosses of non-lactating, non-pregnant mature cows, were used to estimate a standard reference empty body weight (SREBW) for each breed. The SREBW was defined as the empty body weight at skeletal maturity that contained 25% fat. Relationship between empty body fat percentage (EBFP) and empty body weight as a fraction of SREBW (u_E) *was,* $EBFP = -15{\cdot}7 + 40{\cdot}7 * u_E (r^2 = 0{\cdot}77)$. *This relationship was not significantly different among breeds. An evaluation with chemical composition data of five breeds of mature non-lactating cows showed no significant difference in the relationship between EBFP and* u_E. *Data from five experiments showed that cows that lose empty body weight in early lactation had a leaner empty body composition in mid-lactation compared with non-lactating cows at the same value of* u_E. *Equations were formulated to adjust predictions of body composition changes for lactating cows. Copyright © 1996 Elsevier Science Ltd*

INTRODUCTION

Empty body composition of mature cows, measured in terms of weight or percentage of fat, reflects the status of energy reserves in the animal, and this is associated with rebreeding performance (Wettemann *et al.*, 1982; Whitman, 1975). Methods of predicting body composition of mature female cattle would be useful in nutritional management of the cow herd, and in developing models to simulate cow herd productivity. Estimates of a genotype-specific, composition constant target mature body size at skeletal

*To whom correspondence should be addressed.

maturity have been used in formulating models to predict composition of gain in cattle (CSIRO, 1990; Notter, 1977; Sanders & Cartwright, 1979). One common feature of these models is that within each model, genotypes of mature cattle at the same proportion of mature body size have a similar composition. However, body composition at the same proportion of the respective mature body size varies between models. Our first objective was to investigate the composition of empty body weight changes of different breeds of mature female cattle, as a function of mature body size, in experiments where chemical whole body composition was measured. Our second objective was to develop a model to predict composition of empty body weight changes in lactating and non-lactating mature cattle, using relationships obtained from the experimental data.

MATERIALS AND METHODS

General considerations

The model is defined by a set of differential equations written in FORTRAN. Solutions are obtained using a fourth-order Runge–Kutta procedure for numerical integration. Descriptions of state variables and other abbreviations are given in Table 1. Time step in the model is 1 day, and

TABLE 1
Description of variables used in body composition model

Variable	*Units*	*Description*
BW	kg	Bodyweight of animal including weight of contents of gastro-intestinal tract
EBW	kg	Bodyweight of animal excluding weight of contents of gastro-intestinal tract (referred to as empty body weight)
EBFW	kg	Empty body fat weight
EBFFW	kg	Empty body fat-free weight
EBFP	%	Empty body fat percentage
SRBW	kg	Standard reference BW. Body weight of mature cattle when the empty body contains 25% fat
SREBW	kg	Standard reference EBW. Empty body weight of mature cattle that contains 25% fat
u_F	ratio	Stage of maturity for BW (BW/SRBW)
u_E	ratio	Stage of maturity for EBW (EBW/SREBW)
REBFP	%	Reference empty body fat percentage. This is the EBFP calculated with an equation obtained from data on mature non-pregnant, non-lactating cows
REBFW	kg	Reference empty body fat weight (REBFP/100*EBW)
NEB	Mcal	Net energy balance
DIM	day	Days in milk

changes in state variables are denoted by a lower case *d* in front of the state variable.

Experimental data

Chemical empty body composition was obtained on 18 breeds or breed crosses of non-lactating, non-pregnant cows in two experiments. In Experiment 1 (Jenkins *et al.*, 1986), data were collected on 9- and 10-year-old cows produced by mating either Angus or Hereford cows to Angus, Hereford, Red Poll, Brown Swiss (predominantly European), Maine Anjou, Gelbvieh or Chianina sires, (Gregory *et al.*, 1978). Cows produced in a three-breed diallel involving Angus, Hereford and Brown Swiss (predominantly European) that were 6–9 years of age were also included. The experiment commenced 6–8 weeks postweaning when representative cows of each breed were assigned to one of two treatment groups: either fed to maintain body weight (BW), or given *ad libitum* access to an experimental diet (90% maize silage, 9% soybean meal) for 84 days. In addition, representative cows of each breed were slaughtered at the start of the study to provide initial estimates of body composition. These data are described in Table 2.

Breeds in Experiment 2 were Angus, Braunvieh, Charolais, Gelbvieh, Hereford, Limousin, Pinzgauer, Red Poll, and Simmental. These cows were sampled from the Germ Plasm Utilization experiment (Gregory *et al.*, 1991). Within each breed, four cows were assigned to each of four feeding levels of dry matter intake (58, 76, 93, or 111 g/$BW^{0.75}$) of an experimental diet (77·5% ground alfalfa, 17·5% corn, 5% corn silage) with a metabolizable energy content of 2·25 Mcal/kg dry matter (Jenkins & Ferrell, 1994). At the end of a 5-year period, non-pregnant, dry cows continued on their assigned feeding level, and were slaughtered when they were determined to be in BW stasis. This was defined as zero average BW change for eight contiguous weeks. These data are described in Table 3.

In a third experiment (St C. S. Taylor, unpublished data) a total of 18 cattle of the same breed were assigned to different feeding groups and each group was fed a fixed amount of feed for an extended period of time until BW equilibrium was attained. Equilibrium BW in these data was directly proportional to feeding level, and varied from 60 to 140% of composition constant adult body size. All cattle were slaughtered at the end of the experiment and empty body chemical composition was obtained.

Mature body weight and composition

Sanders & Cartwright (1979) and Notter (1977) defined mature body size as the animal's BW at skeletal maturity when live BW and empty BW,

TABLE 2
Breed treatment means for empty body weight (EBW, kg), and empty body fat weight (FAT, kg) of cows in Experiment 1

Breed[a]	*Experimental treatment*[b]								
	Initial slaughter			*Maintenance*			*Ad libitum*		
	n	*EBW*	*FAT*	*n*	*EBW*	*FAT*	*n*	*EBW*	*FAT*
Brown Swiss	2	391	50	4	389	49	5	537	124
Hereford	2	381	55	5	398	80	5	499	139
Angus	4	370	64	5	355	62	5	496	153
Hereford–Angus ×	5	403	82	8	455	114	10	504	145
Red Poll ×	4	376	53	5	385	64	5	463	127
Brown Swiss ×	8	399	59	10	379	49	9	520	138
Gelbvieh ×	4	425	56	6	414	58	6	538	133
Maine Anjou ×	4	436	63	5	445	55	6	564	128
Chianina ×	4	428	60	5	459	66	6	566	136

[a]Hereford–Angus × = 1/2 * (Hereford × Angus + Angus × Hereford), Red Poll × = 1/2 * (Red Poll × Hereford + Red Poll × Angus), etc.
[b]Cows were fed for 84 days a 90% maize-silage, 9% soybean meal diet to maintain body weight (maintenance) or given *ad libitum* access to this diet (*ad libitum*).

TABLE 3

Breed treatment means for empty body weight (EBW, kg) and empty body fat weight (FAT, kg), of cows in Experiment 2

Breed	*Experimental treatment*[a]											
	1			*2*			*3*			*4*		
	n	*EBW*	*FAT*	*n*	*EBW*	*FAT*	*n*	*EBW*	*FAT*	*n*	*EBW*	*FAT*
Hereford	3	488	107	3	486	110	2	584	136	3	579	170
Angus	4	405	81	2	479	164	1	479	113	2	510	162
Red Poll	3	308	28	4	393	73	4	472	138	3	514	152
Braunvieh	2	398	52	3	487	99	3	625	171	3	629	184
Simmental	4	430	44	4	495	82	1	652	170	4	595	136
Limousin	4	397	41	4	498	96	4	556	129	3	608	158
Charolais	3	462	64	4	589	96	3	666	192	2	594	93
Gelbvieh	4	443	49	3	499	101	3	528	98	4	623	135
Pinzgauer	3	439	73	2	472	93	1	680	196	3	600	187

[a]Experimental treatments were daily intake levels of dry matter per kg body weight to the 0·75 power, of a mainly ground alfalfa diet containing 2·25 Mcal ME/kg dry matter, 1 = 58 g, 2 = 76 g, 3 = 93 g, 4 = 111 g.

respectively, contained 25% fat. Taylor & Murray (1991) defined a standard mature BW as adult BW when the proportion of total lipid in the body was 0·25. CSIRO (1990) defined a standard reference weight as the live weight that would be achieved when skeletal maturity is complete and the empty body contains 250 g fat/kg. St C. S. Taylor (unpublished data) defined mature BW as the BW equilibrium of cattle containing 25·1% chemical fat in the empty body.

Body composition varies with gut fill; hence it would be more appropriate to define a genetic mature body size at a fixed adult empty body composition. It would appear that this fixed empty body composition may be arbitrary, and the similarity in adult empty body composition at which mature body size was defined by the above researchers may be due to personal communications and familiarity with previous literature. The only supporting evidence we found for using 25% empty fat was from Robelin (1986), who found that adult male Friesian bulls had about 26% empty body fat at skeletal maturity. However, if these bulls were fed differently, it is possible that they could have achieved a different adult BW and empty body fatness.

Mature BW and degree of maturity for BW may not be appropriate terms when animals are heavier than their mature BW and degree of maturity for BW is greater than 1. In order to avoid the use of terms such as "more mature" and "less mature", the term "standard reference weight" as used by CSIRO (1990), and proportion of standard reference weight will be used to represent mature body size and degree of maturity for mature body size, respectively. Standard reference weight in this study is defined as the adult live BW (SRBW), or adult empty BW (SREBW), when the empty body contains 25% fat.

Predicting body composition of mature cattle

Estimates of SRBW and SREBW for breeds in Experiments 1 and 2 were obtained by regressing empty body fat percentage (EBFP) on empty BW and live BW, respectively, within-breed. Empty body fat percentage was set to 25 in the resulting regression equations, and breed estimates of SRBW and SREBW were calculated. Individual animal data from Experiments 1 and 2 and breed estimates of SRBW and SREBW were used to obtain relationships between EBFP and empty BW and live BW, expressed as a proportion of SRBW and SREBW, respectively. The relationship between EBFP and the proportion of SREBW was evaluated with individual animal data on chemical empty body fat percentages of five breeds of mature cows (Wright & Russel, 1984*a*).

All data used to develop and evaluate the relationship between EBFP and the proportion of SREBW were obtained by chemical analysis of the empty bodies of mature non-lactating cows. Accuracy of this relationship in predicting the empty body fat percentage of lactating mature cows was evaluated with data from five experiments that measured empty body composition of mature lactating cows. Based on the results of this evaluation, a proposal for predicting empty body composition of mature lactating and non-lactating cows is presented.

RESULTS AND DISCUSSION

Estimates of SRBW and SREBW at 25% empty body fat for breeds of adult female cattle in Experiments 1 and 2 are shown in Table 4. Angus cows used in both experiments originated from the same population; hence there was little difference in SREBW between experiments (446 vs. 441 kg). Hereford cows originated from different populations for Experiments 1 and 2, and estimates of SREBW were different (467 vs. 545 kg).

Body weight as a proportion of SRBW (u_F) was calculated for individual animals in both experiments. Breed differences in the slopes of the regressions of EBFP on u_F were not significant. This suggests that at the same value of u_F there were no significant differences in EBFP between breeds in Experiments 1 and 2. Regression equations of EBFP on u_F, obtained with the data in Experiments 1 and 2 are shown below, together with the regression equation obtained by St C. S. Taylor (unpublished data).

TABLE 4

Breed estimates of standard reference body weight (SRBW, kg) and standard reference empty body weight (SREBW, kg) at 25% empty body fat, for adult female cows in Experiments 1 and 2

Experiment 1			*Experiment 2*		
Breed[a]	*SRBW*	*SREBW*	*Breed*	*SRBW*	*SREBW*
Brown Swiss	669	547	Hereford	628	545
Hereford	557	467	Angus	536	441
Angus	542	446	Red Poll	531	456
Hereford–Angus ×	553	461	Braunvieh	675	556
Red Poll ×	572	470	Simmental	744	631
Brown Swiss ×	612	514	Limousin	671	588
Gelbvieh ×	680	557	Charolais	815	693
Maine Anjou ×	787	640	Gelbvieh	803	686
Chianina ×	701	597	Pinzgauer	640	536

[a]Hereford–Angus × = 1/2 * (Hereford × Angus + Angus × Hereford), Red Poll × = 1/2 * (Red Poli × Hereford + Red Poll × Angus), etc.

$$\text{(Taylor) EBFP} = -16{\cdot}8 + 41{\cdot}9 * u_F \ (n = 18, \text{r}^2 = 0{\cdot}76) \tag{1}$$

$$\text{(Exp.1) EBFP} = -17{\cdot}2 + 42{\cdot}2 * u_F \ (n = 156, \text{r}^2 = 0{\cdot}71, \text{SE} = 2{\cdot}2) \tag{2}$$

$$\text{(Exp.2) EBFP} = -19{\cdot}2 + 44{\cdot}5 * u_F \ (n = 108, \text{r}^2 = 0{\cdot}73, \text{SE} = 2{\cdot}7). \tag{3}$$

Body composition and weight data used in these three studies were obtained from 6-year-old or older female cattle. Data used to derive equation (1) were obtained from cattle that were in BW equilibrium; hence this equation gives the relationship between EBFP and u_F for mature cattle that are in BW equilibrium. In Experiment 1, cattle on the low level of feeding may have been in BW equilibrium, but cattle in the initial slaughter group were not in BW equilibrium, and cattle on the high level of feeding were still gaining weight at slaughter. The relationship between EBFP and u_F in equations (1) and (2), was almost identical. These results suggest that the relationship between EBFP and u_F is the same for mature cattle in BW equilibrium or mature cattle that are changing in BW.

Cattle in Experiment 2 were slaughtered when there was little change in BW between consecutive weights, and these cattle may have been in BW equilibrium. The relationship between EBFP and u_F in equation (3) had a greater slope compared to equations (1) and (2). The difference in slopes between equations (2) and (3) may be due to differences in gut fill. This was investigated by calculating empty BW as a proportion of SREBW (u_E), for individual animals, and regressing individual EBFP on u_E. The following regression equations were obtained from this analysis,

$$\text{(Exp.1) EBFP} = -15{\cdot}8 + 40{\cdot}7 * u_E \ (n = 156, \text{r}^2 = 0{\cdot}77, \text{SE} = 1{\cdot}8) \tag{4}$$

$$\text{(Exp.2) EBFP} = -15{\cdot}4 + 40{\cdot}6 * u_E \ (n = 108, \text{r}^2 = 0{\cdot}77, \text{SE} = 2{\cdot}2). \tag{5}$$

The slopes in equations (4) and (5) were almost identical, and this indicates that on an empty BW basis, the relationship between EBFP and u_E in Experiments 1 and 2 was similar. Data from Experiments 1 and 2 were pooled, and individual animal EBFP data was regressed on u_E to obtain the following regression equation:

$$\text{EBFP} = -15{\cdot}7 + 40{\cdot}7 * u_E \ (n = 264, \text{r}^2 = 0{\cdot}77, \text{SE} = 1{\cdot}4). \tag{6}$$

Observed treatment means for EBFP in Experiments 1 and 2 are plotted against treatment means predicted with equation (6) in Fig. 1. The scatter of points in this plot did not depart systematically from the 45-degree line, and this is evidence that the model is a good representation of the real system. Deviations of points from the 45-degree line were greater for Experiment 2 than Experiment 1. Average number of animals/(breed·treatment) in Experiment 1 was 5·8 compared to 3 in Experiment 2 (Table 2 and Table 3), and most of the large deviations in Fig. 1 were from treatments with 1 or 2 animals/(breed·treatment) in Experiment 2.

Predicting composition of empty body weight change

We define empty BW (EBW) as the total weight of fat and fat-free matter; hence if we can predict the fraction of EBW change that is fat, then the composition of this EBW change can be predicted. Equation (6) predicts the EBFP at a given EBW expressed as a proportion of SREBW, and we will refer to this as the reference EBFP (REBFP). We can rewrite equation (6) as:

$$\text{REBFP} = -15{\cdot}7 + 40{\cdot}7 * \text{EBW}/\text{SREBW}$$

where EBW/SREBW is substituted for u_E. Multiplying both sides of this equation by EBW/100, we get:

$$\text{REBFW} = -0{\cdot}157 * \text{EBW} + 0{\cdot}407 * \text{EBW}^2/\text{SREBW}$$

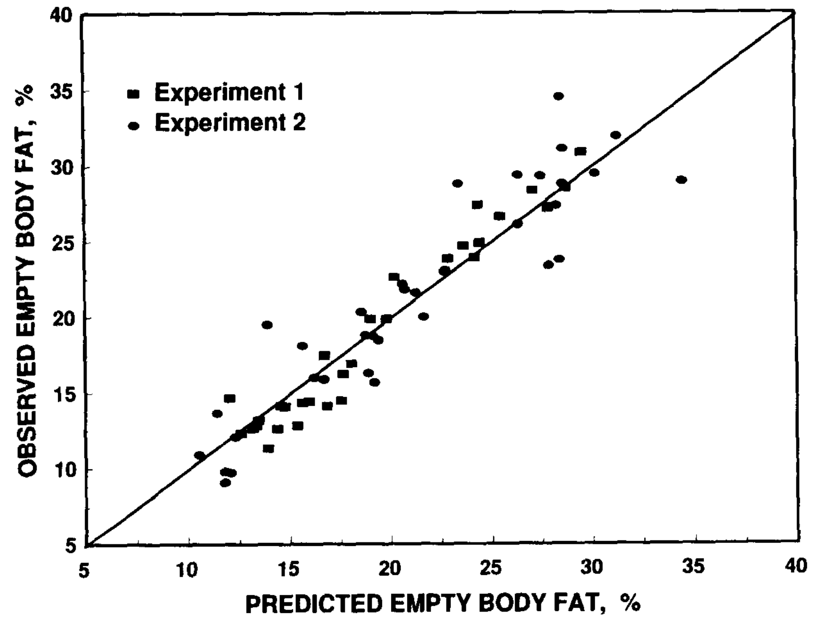

Fig. 1. Observed and predicted empty body fat percentage means for nine breeds by three treatments in Experiment 1 and nine breeds by four treatments in Experiment 2.

where REBFW is the reference empty body fat weight. The instantaneous rate of change in REBFW is given by the first derivative of this equation with respect to EBW.

$$\mathrm{dREBFW/dEBW} = -0{\cdot}157 + 0{\cdot}814 * u_E \tag{7}$$

where u_E is EBW/SREBW. Now by the chain rule for derivatives we can obtain the daily change in REBFW (dREBFW/dt) as:

$$\mathrm{dREBFW}/\mathrm{d}t = \mathrm{dREBFW/dEBW} * \mathrm{dEBW}/\mathrm{d}t. \tag{8}$$

Equation (8) gives the weight of fat in a given daily change in EBW, and in this case the term dREBFW/dEBW represents the fraction of daily EBW change that is fat. If dEBWT/dt = 0, then dREBFW/dt will be zero, and empty body composition will not change. If dEBW/dt = 1, then equations (7) and (8) are equivalent.

Comparisons with other models

The fraction of fat in EBW change was predicted with equation (7) for values of u_E within the range observed in Experiments 1 and 2 (0·6 to 1·31). These predictions were compared to predictions with three published models (CSIRO, 1990; Notter, 1977; Wright & Russel, 1984*b*). With the assumptions of Notter (1977), once an animal attains its SREBW, all changes in EBW are predicted as 100% fat, resulting in mature cows of all breeds having the same composition and the same composition of gain, when evaluated at the same u_E. Wright & Russel (1984*b*) developed the following equation to predict fraction of fat in EBW change:

$$\mathrm{dEBFW/dEBW} = 0 \cdot 186 + 0 \cdot 001036 * \mathrm{EBW}$$

where EBFW is empty body fat weight in kg. According to this equation, the fraction of fat in EBW change is the same for all breeds of mature cattle at the same EBW. However, at the same u_E, EBW of different breeds of mature cattle would be different, and the fraction of fat in EBW change would also be different.

CSIRO (1990) uses one equation to predict g fat/kg EBW change, as a function of dEBW/dt, live BW as a proportion of SRBW, and breed groupings (A, B, or A×B). Breed group B were continental breeds (Charolais, Simmental, Chianina, Maine Anjou, Limousin, Blonde d'Aquitaine), breed group A were other breeds of commercial importance in Australia, and breed group A×B were crossbreds. In this model when live

BW as a proportion of SRBW was greater than 0·6, EBW change had very little impact on the composition of gain, and in predicting the composition of gain we assumed that live BW as a proportion of SRBW was the same as EBW as a proportion of SREBW. According to CSIRO's model, at the same value of u_E, mature cattle of all breeds within a breed group may have different compositions, but the composition of gain would be the same. In addition, the composition of gain for mature cattle at the same value of u_E in different breed groups would be unique to the breed group.

Values for the fraction of fat in EBW change, predicted with equation (7) and the three models above, are plotted against u_E values in Fig. 2. With equation (7) and the model of Notter (1977), there are no breed differences in the composition of EBW change at the same value of u_E. For the models of Wright & Russel (1984*b*), and CSIRO (1990), composition of gain differs between breeds at the same value of u_E, and predicted values for Angus and Charolais cows are shown for these two models. These results show large differences in predicted values for fraction of fat in EBW change between all the models. Equation (7) and Wright & Russel (1984*b*) show a linear increase with increasing values of u_E; Notter (1977) shows no response, and CSIRO (1990) shows a curvilinear response, with very little increase for values of u_E greater than one. At values of u_E less than and greater than 0·96, the composition of EBW change predicted with equation (7) was leaner and fatter, respectively, compared with predictions for Angus cows from Wright & Russel (1984*b*) and CSIRO

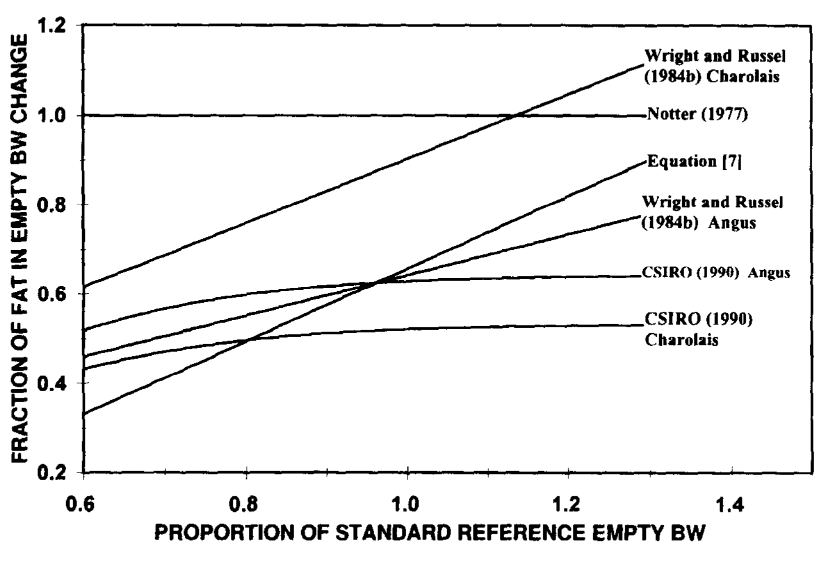

Fig. 2. Predicted values for fraction of fat in empty body weight change, obtained with four models, plotted against proportion of standard reference empty body weight.

(1990). Charolais cattle had greater amounts of fat in EBW change than Angus cattle with the model of Wright & Russel (1984*b*), and the opposite was true for the model of CSIRO (1990). In the model of Wright & Russel (1984*b*), at the same value of u_E, larger and leaner breeds of cattle were heavier and had a greater proportion of fat in EBW change than smaller and fatter breeds of cattle. For values of u_E ranging from 0·6 to 1·3, the fraction of fat in EBW change increased from 0·657 to 0·901 with equation (7), and from 0·630 to 0·641 and 0·521 to 0·531 for Angus and Charolais cows, respectively, with the model of CSIRO (1990).

Evaluation

Individual animal data on the chemical composition of the empty bodies of 73 non-lactating mature cows representing five breeds (Wright & Russel, 1984*a*) were used to evaluate equation (6). Breed values of SREBW were estimated from within-breed regressions of EBFP on EBW, and values for u_E were calculated for each animal in these data. Data from Experiments 1 and 2 used to obtain equation (6) were classified as Trial 1, and data from Wright & Russel (1984*a*) were classified as Trial 2. Heterogeneity of slopes of the within-trial regression of EBFP on u_E was tested with the following linear model:

$$y_{ij} = \mu + T_i + bU_{ij} + c_iU_{ij} + e_{ij}$$

where y_{ij} is the jth observation of EBFP within the ith trial, T_i is an effect due to the ith trial, b is the linear regression coefficient for EBFP on U_{ij}, c_i is the within-trial linear regression coefficient expressed as a deviation from the average linear regression of EBFP on U_{ij}, and U_{ij} is the value of u_E for the jth animal in the ith trial. Results of this analysis showed no evidence that the slopes of the regression of EBFP on u_E within-trial were different.

Observed values for EBFP for the data of Wright & Russel (1984*a*) are plotted against EBFP values predicted with equation (6) in Fig. 3. The scatter of points in this plot did not depart systematically from the 45-degree line, providing further evidence that equation (6) closely represents the underlying relationship between EBFP and u_E in non-lactating mature cows.

All data used in the development and evaluation of equation (6) and also St C. S. Taylor (unpublished data), were obtained through chemical analysis of the empty bodies of non-lactating mature cows. If a given amount of EBW change in non-lactating and lactating cows has the same composition, then equations (6) and (7) could be used to predict empty body composition, and composition of EBW change, respectively, in lactating and non-lactating cows. Results on prepartum and postpartum cows reviewed by Bauman & Currie (1980) and McNamara (1991) indicate that several physiological changes that promote increased lipolysis and decreased lipogenesis begin to occur 30 days prepartum and continue into the postpartum period. If these physiological changes result in a greater proportion of fat in EBW change of cows during early lactation, compared to non-lactating cows at the same value of u_E, then equation (6) would overpredict the percentage of fat in early lactation cows that have lost EBW.

Equation (6) was evaluated with empty body composition data on lactating cows obtained by chemical analysis (Andrew *et al.*, 1994; Gibb *et al.*, 1992; McGuffey *et al.*, 1991), carcass-specific gravity (Bath *et al.*, 1965), and chemical analysis of the non-carcass combined with carcass-specific gravity (Brown *et al.*, 1989). Data from Gibb *et al.* (1992) were on British Holstein–Friesian cows, and all other data were on American Holstein cows. Data on chemical empty body composition of five 6–12-year-old Holstein cows (Ellenberger *et al.*, 1950) were used to obtain an estimate of SREBW. The regression equation of EBFP on EBW in these data was $\text{EBFP} = -23 \cdot 5 + 0 \cdot 0935 * \text{EBW}$ ($n = 5$, $r^2 = 0{\cdot}96$, $\text{SE} = 0{\cdot}01$), and the estimate of SREBW was 519 kg. These data were obtained from cows in the 1940s, and we increased the estimate of SREBW by 5% for Holstein cows in the 1980s (SREBW = 545 kg). Data from a trial in

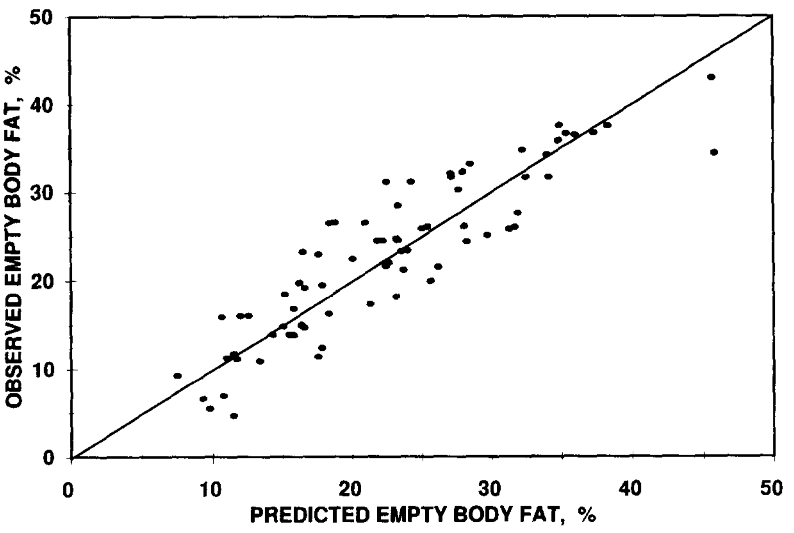

Fig. 3. Observed individual animal empty body fat percentage ($n = 73$) from the experiment of Wright & Russel (1984*a*), and predicted individual empty body fat percentage from equation (6).

Poland that included Friesians from USA and the UK (Jasiorowski *et al.*, 1983) showed that American Friesians were about 6% bigger than British Friesians, and a SREBW value of 512 kg was used for the data of Gibb *et al.* (1992).

Data from the above five experiments are shown in Table 5, along with EBFP predicted with equation (6). For just-calved (0 days in milk; DIM) and 7-day prepartum cows, equation (6) accurately predicted EBFP. For the other 10 treatment groups in these five experiments, equation (6) consistently overpredicted EBFP for lactating cows. These results show that the model for non-lactating mature cows could accurately predict EBFP of mature cows that have just calved or are at a very advanced stage of pregnancy, but would overpredict the EBFP in lactating cows. Results were further interpreted to suggest that lactating cows would have a greater proportion of fat in EBW change than that predicted with equation (7).

Williams *et al.* (1989) used the concept that lactating cows have a greater proportion of fat in EBW change compared with non-lactating cows, to develop a model that predicted the fraction of fat in EBW loss of Holstein cows during early lactation. The fraction of fat in EBW loss of Holstein cows (SREBW = 545 kg) predicted with equation (7) and with the model of Williams *et al.* (1989) are plotted against values of u_E ranging from 0·6 to 1·3 in Fig. 4. The fraction of fat in EBW change with Williams *et al.* (1989) is a function of EBW, and EBW values were obtained by multiplying SREBW by u_E. Compared with equation (7), the fraction of

TABLE 5

Observed and predicted average empty body fat percentage of prepartum, just calved, and lactating mature Holstein cows

Source	*n*	*Days in milk*	*Empty body wt, kg*	*Empty body fat, %*	
				Observed	*Predicted*[a]
Bath *et al.* (1965)	6	42	454	14·2	18·2
	6	91	417	11·8	15·4
	5	147	397	9·1	13·9
Brown *et al.* (1989)	9	126	471	11·3	19·5
McGuffey *et al.* (1991)	12	36	470	16·3	19·4
Gibb *et al.* (1992)	6	0	500	22·1	24·0
	6	14	471	18·4	21·7
	6	35	459	19·6	20·8
	6	42	444	16·5	19·6
Andrew *et al.* (1994)	10	−7	463	19·4	18·9
	7	63	452	10·5	18·1
	8	269	480	16·9	20·1

[a]Empty body fat percentage predicted with equation (6), using a value of 512 kg for SREBW of cows from the experiment by Gibb *et al.* (1992), and 545 kg for the other experiments.

fat in EBW loss predicted with Williams *et al.* (1989) was 1·6 times greater at a u_E value of 0·6 and 1·1 times greater at a u_E value of 1·3. One major limitation of Williams *et al.* (1989) is that the model is based on a single breed and cannot be extrapolated to other breeds. Another consequence of Williams *et al.* (1989) is that the model would predict different fractions of fat in EBW change, between mature cows of different breeds at the same value of u_E, and this result is the opposite of that in equation (7).

We conclude from this evaluation that for different breeds of cattle, equation (7) would adequately predict the fraction of fat in EBW change of non-lactating cows, but would underpredict this fraction during lactation. One solution would be to use non-lactating cows as a base, and for lactating cows, adjust upwards the fraction of fat predicted with equation (7). This approach is discussed in the following section.

Modelling composition of empty body weight changes in lactating and non-lactating mature cattle

Equation (7) may be modified additively or multiplicatively to predict a higher proportion of fat in EBW change during lactation. We chose to use an additive adjustment. Equation (7) is dREBFW/dEBW $= -0{\cdot}157 + 0{\cdot}814 * u_E$, and with an additive adjustment we will predict the fraction of fat in EBW change (dEBFW/dEBW) as dREBFW/dEBW, plus an

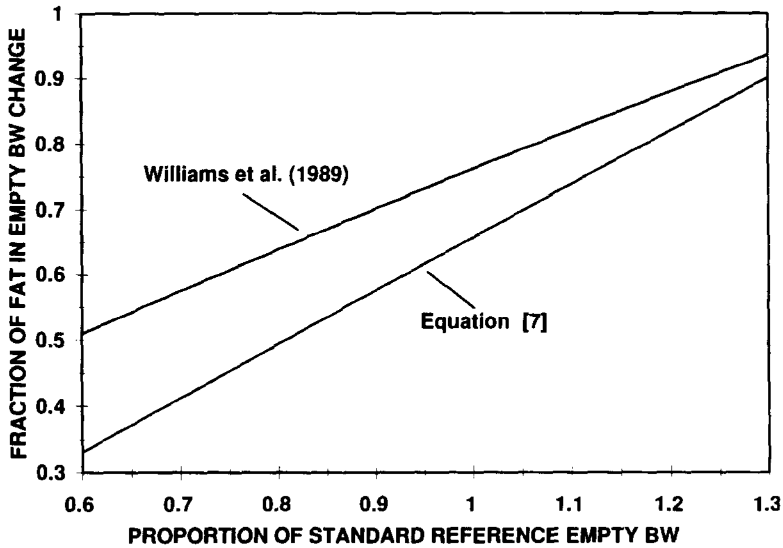

Fig. 4. Fraction of fat in empty body weight change, predicted with the model of Williams *et al.* (1989) for lactating Holstein cows, and with equation (7) for non-pregnant non-lactating mature cows, plotted against proportion standard reference empty body weight.

additional fraction which will be smaller than dREBFW/dEBW. For non-lactating cows the additive adjustment will be zero, and in this case dEBFW/dEBW = dREBFW/dEBW. The additive adjustment may be fixed, or we can use a non-linear function based on DIM gradually to increase it from zero at the start of lactation to some peak value, then decrease it. Studies by Bauman & Currie (1980) and Hart (1983) tend to support a non-linear additive adjustment based on DIM.

Data from Hart (1983) show that circulating concentrations of growth hormone increase and concentrations of insulin decrease with the magnitude of negative energy balance during early lactation. Data from Moe (1965), reviewed by Bauman & Currie (1980), show that net energy balance in six high-producing dairy cows was lowest (approximately −9 Mcal/day) between weeks 1 and 4 of lactation, after which net energy balance started to increase. We assume that lactating cows in negative energy balance would lose EBW, and these data suggest that the fraction of fat in EBW loss would increase as net energy balance becomes more negative.

The incomplete gamma function may be a reasonable function for an additive adjustment, because it has the properties needed to make the adjustment increase from zero at the start of lactation to some peak value, then decrease it as the lactation progresses. This function is given in the following equation:

$$\lambda = a * n^b * e^{-cn}$$

where n is DIM, and a, b, and c are parameters. Peak value for λ is obtained when $n = b/c$. Wood (1967) used this function to predict daily milk yields, whereas we are using it to calculate an additive adjustment.

The value of λ would be the same for all values of u_E at the same DIM, whereas predictions with the model of Williams *et al.* (1989) in Fig. 4, show that the difference in dEBFW/dEBW between lactating and non-lactating cows decreases as u_E increases. It is also possible for dEBFW/dEBW to be greater than 1 if the value of λ remains independent of u_E; hence, we propose that λ should be corrected for u_E. The value of dREBFW/dEBW increases with increasing values of u_E, and a simple functional form to correct λ for u_E would be 1 − dREBFW/dEBW. With this correction we get:

$$\text{dEBFW/dEBW} = \text{BASE} + (1 - \text{BASE}) * \lambda \tag{9}$$

where BASE = dREBFW/dEBW. According to equation (9), lactating cows in negative energy balance would mobilize fat reserves, and EBFW would decrease at a faster rate than REBFW predicted with equation (6).

We propose that for extended periods of negative energy balance, these cows would start to conserve energy by reducing the fraction of fat in EBW loss predicted with equation (9), and this would result in reduced daily milk yields. The following modification of equation (9) is suggested to account for this tendency to conserve energy:

$$\mathrm{dEBFW/dEBW} = \mathrm{BASE} + (1 - \mathrm{BASE}) * \lambda * \mathrm{EBFW/REBFW} \qquad (10)$$

where EBFW is the actual weight in kg of empty body fat and REBFW is the reference empty body fat weight in kg predicted with equation (6).

The next case to consider is where lactating cows that lose EBW during early lactation start to gain EBW later on in the lactation. Data from Flatt *et al.* (1965) summarized by Reid & Robb (1971) show that cows that lose EBW and deplete fat reserves during early lactation, replete these fat reserves when EBW change becomes positive. Data from Chigaru & Topps (1981) on lactating Hereford × British Friesian mature cows that lost EBW between day 70 and 112 of lactation, and fully regained the EBW loss at day 154 of lactation, showed that empty body composition at day 154 was approximately the same as at day 70. Data from Gibb *et al.* (1992) on chemical empty body composition of 54 Holstein–Friesian cows, slaughtered serially at 0, 2, 5, 8, 11, 14, 19, 24, and 29 weeks postpartum, showed that 37·4 kg fat was depleted between 0 and 8 weeks postpartum, and at 24 weeks postpartum both EBW and fat weight were approximately the same as at 0 weeks postpartum. These data indicate that when EBW lost in early lactation is fully regained in late lactation, the weight of fat depleted is also fully regained. For cows that are gaining EBW after a period of EBW loss during early lactation, we propose the following equation to predict the fraction of fat in daily EBW gain:

$$\mathrm{dEBFW/dEBW} = \mathrm{BASE} * \mathrm{REBFW/EBFW}. \qquad (11)$$

At the end of the EBW loss period REBFW would be greater than EBFW and the quantity REBFW/EBFW would be greater than 1. Hence, equation (11) would predict a higher fraction of fat in EBW gain than BASE predicted with equation (7), and over the EBW gain period, empty body composition would gradually approach the composition at the start of the EBW loss period.

Equations (10) and (11) both predict the fraction of fat in EBW change. Equation (11) was developed for lactating cows that are gaining EBW after a period of EBW loss, and equation (10) for lactating cows that are losing EBW, and non-lactating cows that are either gaining or losing EBW. For non-lactating cows, DIM is zero, and λ is zero; hence dEBFW/dEBW = BASE = dREBFW/dEBW. Both equations (10) and (11) predict dEBFW/dEBW, and the daily change in weight of fat is:

$$\mathrm{dEBFW}/\mathrm{d}t = \mathrm{dEBFW}/\mathrm{dEBW} * \mathrm{dEBW}/\mathrm{d}t. \tag{12}$$

According to this equation empty body composition would not change when animals are in weight stasis ($\mathrm{dEBW}/\mathrm{d}t = 0$). We will discuss the impact of equation (12) on body composition of cows that lose EBW during early lactation and do not fully regain the weight loss at the end of lactation. In the first case if we feed these cows at the end of lactation to maintain EBW, empty body composition would not change and EBFW would remain smaller than REBFW (predicted with equation (6)) regardless of the duration of weight stasis. In the second case if we feed these cows to regain EBW loss fully during the dry period, the weight of fat lost would not be fully regained. In these cows EBFW is less than REBFW at the end of lactation, and we propose that if these cows are kept in EBW stasis or are fed in the dry period to regain the EBW loss, then EBFW would gradually approach REBFW. This proposal is incorporated into equation (12) with the following modification:

$$\mathrm{dEBFW}/\mathrm{d}t = \mathrm{dEBFW}/\mathrm{dEBW} * \mathrm{dEBW}/\mathrm{d}t + 0{\cdot}003 * (\mathrm{REBFW} - \mathrm{EBFW}) \tag{13}$$

where REBFW is predicted with equation (6) and EBFW is actual weight of fat. The constant 0·003 is based on experimental results of Taylor *et al.* (1981) who found that fixed levels of feeding need to be maintained for approximately 2 years before an equilibrium BW is achieved.

The mathematical formulation of a model to predict composition of EBW change in lactating and non-lactating cows is contained in equation (13), where dEBFW/dEBW is predicted with equation (11) for lactating cows that are gaining EBW, or with equation (10) for all other cows. The next step is to estimate parameters a, b, and c, used to calculate λ. Data on Hereford × British Friesian mature cows from Chigaru & Topps (1981) summarized by Williams *et al.* (1989) were used to estimate parameters a, b, and c. These cows lost an average of 37 kg BW and 21·56 kg fat from 70 to 112 days of lactation. Values for the parameters a, b, and c, were calibrated to fit these data. The resulting values were $a = 0{\cdot}001$, $b = 2$, and $c = 0{\cdot}045$. From 112 to 154 days of lactation, the cows in this experiment fully regained BW lost during days 70 to 112 of lactation. Simulated results using equation (13) and the values for parameters a, b, and c showed that these cows regained 21·21 kg fat, compared with an average observed value of 21·73 kg fat.

Angus cows at SREBW ($u_E = 1$) were simulated to lose 1 kg EBW in the first 100 days of lactation, using equation (13) to predict the fraction of fat in daily EBW loss over this period. The fraction of fat in daily EBW loss from this simulation and from equation (7) are plotted against DIM in Fig. 5. These results show that over the period simulated, weight loss contained 64·7% fat with equation (13) vs. 56·7% with equation (7). The fraction of fat in EBW loss predicted with equation (13) peaked at 34 DIM, and the curve had a similar opposite shape to the net energy balance curve calculated by Bauman & Currie (1980) with data from Moe (1965) on six Holstein cows.

The value of λ in equation (10) can be increased or decreased by changing the value of the parameter a; hence, it is possible that we may be able to calibrate this parameter to reflect the magnitude of negative energy balance in lactating cows. The magnitude of negative energy balance during early lactation is probably greater in dairy cows than in beef cows, and this calibration may be more applicable for dairy cows. However, reproducing beef cows consume lower quality diets than dairy cows, and this would justify calibrating parameter a for beef cows also. In Fig. 6, λ values for $a = 0{\cdot}001$ and $0{\cdot}0012$ are plotted against DIM. For the first 100 days of lactation the average λ value was 0·18 with $a = 0{\cdot}001$ and 0·22 with $a = 0{\cdot}0012$. At 150 DIM, λ values were small and had very little impact on the added fraction of fat in EBW loss predicted with equation (13).

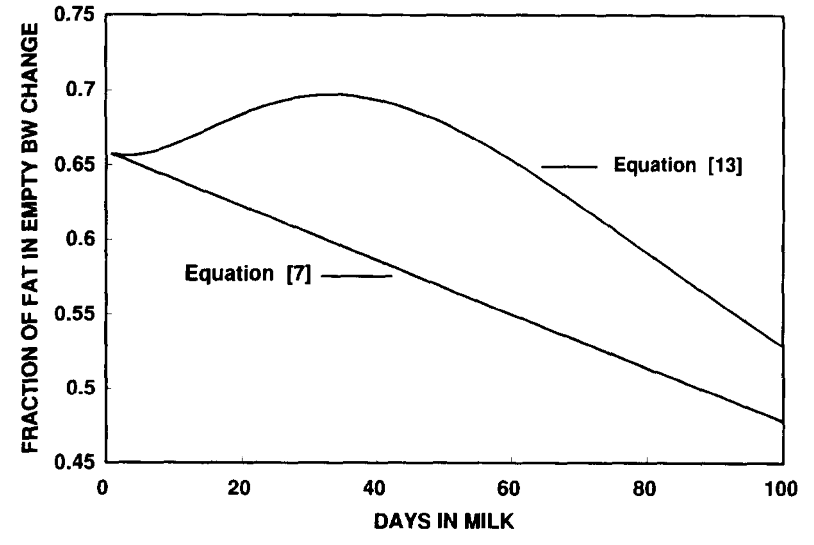

Fig. 5. Relationship between fraction of fat in empty body weight change, predicted with equations (7) and (11), and days in milk, for Angus cows losing 1 kg empty body weight per day, over the first 100 days of lactation.

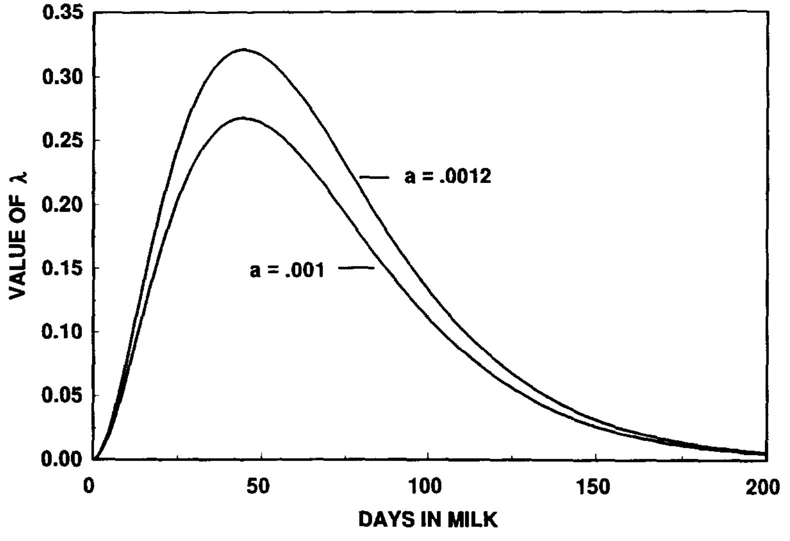

Fig. 6. Relationship between λ values and days in milk, at two values for the parameter a, $\lambda = a * n^b * e^{-cn}$, where n is days in milk, $b = 2$, and $c = 0{\cdot}045$.

APPLICATION

Models that simulate cattle performance (Bourdon, 1983; Notter, 1977) use predicted daily feed intake as the starting point, and estimate the daily net energy balance which may be negative or positive after accounting for energy requirements for maintenance, gestation, and lactation. This daily net energy balance (dNEB/dt) is used in the aforementioned models to predict the amount and composition of daily changes in EBW. Equations developed in the present study are driven by daily rates of change in EBW which impact EBW as a proportion of SREBW, and we will show how dNEB/dt can be used to drive these equations and predict the amount and composition of EBW changes, then work through an example to illustrate the methodology.

Daily change in EBW is composed of fat (dEBFW/dt) and fat-free matter (dEBFFW/dt). All of dEBFW/dt contains energy, but only the protein fraction of dEBFFW/dt contains energy. We will use 9·5 Mcal and 5·7 Mcal (Brouwer, 1965) as the net energy value per kg of fat and protein, respectively, and assume that dEBFFW/dt contains 24·3% protein (Williams *et al.*, 1995). Because dEBW/dt = dEBFFW/dt + dEBFW/dt, we can write dEBFFW/dt as dEBW/dt − dEBFW/dt. Hence,

$$\mathrm{dNEB}/\mathrm{d}t = p * (\mathrm{dEBW}/\mathrm{d}t - \mathrm{dEBFW}/\mathrm{d}t) + f * \mathrm{dEBFW}/\mathrm{d}t$$

where $p = 0{\cdot}243 * 5{\cdot}7 = 1{\cdot}39$, and $f = 9{\cdot}5$. This equation contains two unknowns (dEBW/dt and dEBFW/dt), and in order to obtain a solution we will rewrite dEBFW/dt in terms of dEBW/dt, to obtain one equation with one unknown, which is dEBW/dt.

Equation (13) is used to predict dEBFW/dt, and this equation can be rewritten as

$$\mathrm{dEBFW}/\mathrm{d}t = k * \mathrm{dEBW}/\mathrm{d}t + q$$

where $q = 0 \cdot 003 * (\mathrm{REBFW} - \mathrm{EBFW})$ and $k = \mathrm{dEBFW}/\mathrm{dEBW}$, which is calculated with equation (10) or equation (11). Substituting this equation for dEBFW/dt into the equation for dNEB/dt we get

$$\begin{aligned}\mathrm{dNEB}/\mathrm{d}t &= p * (\mathrm{dEBW}/\mathrm{d}t - (k * \mathrm{dEBW}/\mathrm{d}t + q)) + f * (k * \mathrm{dEBW}/\mathrm{d}t + q) \\ &= p * \mathrm{dEBW}/\mathrm{d}t - p * k * \mathrm{dEBW}/\mathrm{d}t - p * q + f * k * \mathrm{dEBW}/\mathrm{d}t + f * q \\ &= \mathrm{dEBW}/\mathrm{d}t * (p - p * k + f * k) - p * q + f * q \qquad (14)\end{aligned}$$

and

$$\mathrm{dEBW}/\mathrm{d}t = (\mathrm{dNEB}/\mathrm{d}t + p * q - f * q)/(p - p * k + f * k). \qquad (15)$$

The knowns in this equation are dNEB/dt, p and f. The unknowns are k and q. If animals are lactating, k is calculated with equation (10) for dEBW/d$t < 0$ and equation (11) for dEBW/d$t > 0$. Hence we need to calculate the value of dNEB/dt at which dEBW/dt is zero. This value is obtained by setting dEBW/dt to zero in equation (14) and calculating the value of dNEB/dt as dNEB/d$t = f * q - p * q$. If dNEB/dt is greater than this value then equation (11) is used, and if it is less than this value equation (10) is used. The following example illustrates the estimation of k and q.

The example is based on a Hereford × Angus cow (SREBW = 461 kg, from Table 2), 10 DIM, with an EBW of 378 kg, 15% empty body fat, and a dNEB/dt of −3 Mcal. These five pieces of information are all that is needed to estimate the amount and composition of dEBW/dt. For different genotypes values of SREBW in Table 2 can be used. DIM and EBW are known. The simulation model being used would keep track of empty body fat percentage and estimate dNEB/dt on a daily basis. With this information values for the following variables are calculated as follows:

$$u_E = \mathrm{EBW}/\mathrm{SREBW} = 378/461 = 0{\cdot}82$$

$$\lambda = 0{\cdot}001 * 10^2 * e^{-0045*10} = 0{\cdot}0638$$

$$\text{EBFW} = 0{\cdot}15 * 378 = 56{\cdot}7 \text{ kg (weight of empty body fat).}$$

From equation (6) the reference empty body fat percentage (REBFP) is

$$\text{REBFP} = -15{\cdot}7 + 40{\cdot}7 * \text{EBW/SREBW} = 17{\cdot}674$$

$$\text{REBFW} = 0{\cdot}17674 * 378 = 66{\cdot}8 \text{ kg (reference empty body fat weight)}$$

$$\text{BASE} = -0{\cdot}157 + 0{\cdot}814 * u_E = 0{\cdot}5105 \text{ [eqn(7)]}$$

$$q = 0{\cdot}003 * (66{\cdot}8 - 56{\cdot}7) = 0{\cdot}0303.$$

The value of dNEB/dt for zero change in EBW is (9·5*0·0303−1·39*0·0303) = 0·2458. Because the actual value of dNEB/dt is −3, and DIM is 10, we will use equation (10) to calculate k. With this equation we get:

$$k = 0{\cdot}5105 + (1 - 0{\cdot}5105) * 0{\cdot}0638 * 56{\cdot}7/66{\cdot}8 = 0{\cdot}537$$

and with equation (15) we get:

$$\text{dEBW/d}t = (-3 + 1{\cdot}39 * 0{\cdot}0303 - 9{\cdot}5 * 0{\cdot}0303)/$$

$$(1{\cdot}39 - 1{\cdot}39 * 0{\cdot}537 + 9{\cdot}5 * 0{\cdot}537) = -0{\cdot}565 \text{ kg}$$

$$\text{dEBFW/d}t = 0{\cdot}537 * (-0{\cdot}565) + 0{\cdot}0303 = -0{\cdot}273 \text{ kg}$$

$$\text{dFFMW/d}t = -0{\cdot}565 - (-0{\cdot}273) = -0{\cdot}292.$$

The fraction of fat in this weight loss is −0·273/−0·565 = 0·4832, and the energy contained in the weight loss is 3 Mcal (1·39*0·292 + 9·5*0·273) or 5·309 Mcal/kg weight loss (3/0·565).

Empty body weight loss to satisfy a negative energy balance of 3 Mcal of net energy was calculated for this cow at 15% and 17% empty body fatness, and 1 at its SREBW of 461 kg and an empty body fatness of 25%. These calculations were made at 10, 30, and 150 DIM, and during the dry period, and the results together with the energy density of the weight loss are shown in Table 6. At 30 DIM the energy density of the weight loss is higher than at 10 DIM and the weight loss is smaller. Weight losses have the lowest energy density late in the lactation (150 DIM) and during the

TABLE 6
Daily amount[a] (kg) and energy density (Mcal/kg) of empty body weight loss to satisfy a negative net energy balance of 3 Mcal for a cow with a standard reference empty body weight of 461 kg in different physiological states

Animal description[b]	*Days of lactation*			
	10	*30*	*150*	*Dry*
378 kg, 15% fat				
Weight loss (kg)	−0·565	−0·514	−0·578	−0·587
Energy/kg weight loss (Mcal)	5·309	5·838	5·193	5·111
378 kg, 17% fat				
Weight loss (kg)	−0·530	−0·477	−0·544	−0·554
Energy/kg weight loss (Mcal)	5·657	6·291	5·517	5·418
461 kg, 25% fat				
Weight loss (kg)	−0·435	−0·407	−0·442	−0·447
Energy/kg weight loss (Mcal)	6·896	7·367	6·792	6·718

[a]With an actual simulation, daily net energy balance and amount and energy density of empty body weight loss would change each day.
[b]All weights and fatness are on an empty body weight basis.

dry period. In addition, if the animal was fatter (17%), the weight loss would have a higher energy density; thus a smaller weight loss would be required to satisfy the same negative energy balance, compared with an animal at 15% empty body fatness. This trend is seen to a greater extent in animals that are heavier and fatter (461 kg with 25% empty body fat), and supports results which show that animals that are in good condition at calving tend to have shorter post-calving intervals, compared with animals that calve in poor condition.

For a larger breed of cow at the same proportion of SREBW and at the same percentage empty body fatness as a smaller type, the weight loss to satisfy the same negative energy balance would have approximately the same energy density. Therefore the smaller type would have an advantage under conditions of low-feed availability, because of its lower total maintenance requirements. The equations in this paper can also be used to calculate the net energy requirements for a specified daily gain. In this case $dEBWT/dt$ is known, and equation (14) would predict the daily net energy requirements for empty body weight gain.

REFERENCES

Andrew, S. M., Waldo, D. R. & Erdman, R. A. (1994). Direct analysis of body composition of dairy cows at three physiological stages. *Journal of Dairy Science*, **77**, 3022–3033.

Bath, D. L., Ronning, M., Meyer, J. H. & Lofgreen, G. P. (1965). Caloric equivalent of live weight loss of dairy cattle. *Journal of Dairy Science*, **48**, 374–380.
Bauman, D. E. & Currie, W. B. (1980). Partitioning of nutrients during pregnancy and lactation: a review of mechanisms involving homeostasis and homeorhesis. *Journal of Dairy Science*, **63**, 1514–1529.
Bourdon, R. M. (1983). Simulated effects of genotype and management on beef production efficiency. PhD dissertation. Colorado State University, Fort Collins, USA.
Brouwer, E. (1965). Report of sub-committee on constants and factors. In Energy Metabolism, ed. K. L. Blaxter. Troon, European Association for Animal Production, Publ. No. 11, pp. 441–444.
Brown, D. L., Taylor, S. J., De Peters, E. J. & Baldwin, R. L. (1989). Influence of Sometribove, USAN (recombinant methionyl bovine somatotropin) on the body composition of lactating cattle. *Journal of Nutrition*, **119**, 633–638.
Chigaru, P. R. N. & Topps, J. H. (1981). The composition of body-weight changes in underfed lactating beef cows. *Animal Production*, **32**, 95–103.
CSIRO (1990). Feeding standards for Australian livestock. Ruminant, eds G. E. Robards and J. C. Radcliffe. Australian Agricultural Council, Ruminants Sub-committee. CSIRO Publications, Victoria, Australia, pp. 41–46.
Ellenberger, H. B., Newlander, J. A. & Jones, C. H. (1950). Composition of the bodies of dairy cattle. *Vermont Agricultural Experimental Station Bulletin*, **558**, 1–66.
Flatt, W. P., Moore, L. A., Hooven, N. W. & Plowman, R. D. (1965). Energy metabolism studies with a high producing lactating dairy cow (Abstract). *Journal of Dairy Science*, **48**, 797.
Gibb, M. J., Ivings, W. E., Dhanoa, M. S. & Sutton, J. D. (1992). Changes in body components of autumn-calving Holstein–Friesian cows over the first 29 weeks of lactation. *Animal Production*, **55**, 339–360.
Gregory, K. E., Cundiff, L. V., Smith, G. M., Laster, D. B. & Fitzhugh, H. A., Jr. (1978). Characterization of biological types of cattle — Cycle II: I. Birth and weaning traits. *Journal of Animal Science*, **47**, 1022–1030.
Gregory, K. E., Cundiff, L. V. & Koch, R. M. (1991). Breed effects and heterosis in advanced generations of composite populations for preweaning traits of beef. *Journal of Animal Science*, **69**, 947–960.
Hart, I. C. (1983). Endocrine control of nutrient partitioning in lactating ruminants. *Proceedings of the Nutrition Society*, **42**, 181–194.
Jasiorowski, H., Reklewski, Z. & Stolzman, M. (1983). Testing of different strains of Friesian cattle in Poland. I. Milk performance of F_1 paternal Friesian strain crosses under intensive feeding conditions. *Livestock Production Science*, **10**, 109–122.
Jenkins, T. G., Ferrell, C. L. & Cundiff, L. V. (1986). Relationship of components of the body among mature cows as related to size, lactation potential and possible effects on productivity. *Animal Production*, **43**, 245–254.
Jenkins, T. G. & Ferrell, C. L. (1994). Productivity through weaning of nine breeds of cattle under varying feed availabilities: I. Initial evaluation. *Journal of Animal Science*, **72**, 2787–2797.
McGuffey, R. K., Basson, R. P. & Spike, T. E. (1991). Lactation response and body composition of cows receiving Somatotropin and three ratios of forage to concentrate. *Journal of Dairy Science*, **74**, 3095–3102.

McNamara, J. P. (1991). Regulation of adipose tissue metabolism in support of lactation. *Journal of Dairy Science*, **74**, 706–719.

Moe, P. W. (1965). Effects of level of intake on the utilization of diets by dairy cows. PhD thesis. Cornell University, Ithaca, NY, USA.

Notter, D. R. (1977). Simulated efficiency of beef production for a cow-calf-feedlot management system. PhD dissertation. University of Nebraska, Lincoln, USA.

Reid, J. T. & Robb, J. (1971). Relationship of body composition to energy intake and energetic efficiency. *Journal of Dairy Science*, **54**, 533–564.

Robelin, J. (1986). Growth of adipose tissue in cattle: partitioning between depots, chemical composition and cellularity. A review . *Livestock Production Science*, **14**, 349–364.

Sanders, J. O. & Cartwright, T. C. (1979). A general cattle production systems model. Part II: Procedures used for simulating animal performance. *Agricultural Systems*, **4**, 289–309.

Taylor, St C. S. & Murray, J. I. (1991). Effect of feeding level, breed and milking potential on body tissues and organs of mature, nonlactating cows. *Animal Production*, **53**, 27–38.

Taylor, St C. S., Turner, H. G. & Young, G. B. (1981). Genetic control of equilibrium maintenance efficiency in cattle. *Animal Production*, **33**, 179–194.

Wettemann, R. P., Lusby, K. S. & Turman, E. J. (1982). Relationship between changes in prepartum weight and condition and reproductive performance of range cows. *Oklahoma Agricultural Experimental Station Bulletin*, **112**, 12–15.

Whitman, R. W. (1975). Weight change, body condition and beef-cow reproduction. PhD dissertation. Colorado State University, Fort Collins, USA.

Williams, C. B., Oltenacu, P. A. & Sniffen, C. J. (1989). Refinements in determining the energy value of body tissue reserves and tissue gains from growth. *Journal of Dairy Science*, **72**, 264–269.

Williams, C. B., Bennett, G. L. & Keele, J. W. (1995). Simulated influence of postweaning production system on performance of different biological types of cattle: III. Biological efficiency. *Journal of Animal Science.*, **73**, 585–698.

Wood, P. D. P. (1967). Algebraic model of the lactation curve in cattle. *Nature*, **216**, 164–165.

Wright, I. A. & Russel, A. J. F. (1984*a*). Partition of fat, body composition and body condition score in mature cows. *Animal Production*, **38**, 23–32.

Wright, I. A. & Russel, A. J. F. (1984*b*). The composition and energy content of empty- body-weight change in mature cattle. *Animal Production*, **39**, 365–369.